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ORIGINAL PAPER

Spatiotemporal variation and sediment retention effects on nematode communities associated with *Halimeda opuntia* (Linnaeus) Lamouroux (1816) and *Sargassum polyceratium* Montagne (1837) seaweeds in a tropical phytal ecosystem

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Abstract Nematodes play an important role in ecological processes and are one of the most abundant meiofaunal organisms associated with seaweeds. Yet, knowledge on seaweed bed ecosystems is limited. Nematodes associated with *Sargassum polyceratium* and *Halimeda opuntia* were compared in two transects, 80 m apart and parallel to the beach line in Cupe Beach, Brazil. The temporal variation during the dry and rainy seasons and the effect of sediment retention by the seaweed on nematode density and composition were investigated. The differences in nematode communities between the two seasons were mainly caused by the increase in density of the most abundant genera in the rainy season. A significant difference was observed between the nematode communities of the two transects for *H. opuntia*. The nematode communities of both seaweed species did not differ significantly in the same transect. The genus *Euchromadora* was dominant in both seaweed species. The amount of sediment retained by the seaweeds did not affect the overall nematode density. However, it was positively correlated with the density of *Draconema* and *Euchromadora* in both seaweeds, and both genera were exclusively found associated with seaweeds. This result opposes the idea that the more sediment retained by the seaweed, the higher the nematode overall density and the higher the number of nematodes originally coming from the sediment.

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Introduction

Seaweed beds and associated fauna form a highly productive ecosystem in shallow water coastal areas (De Troch et al. 2001). Seaweeds harbor a variety of organisms belonging to almost all trophic levels of the food web and also serve as a shelter, reproduction and/or grazing site for many organisms (Brewer et al. 1994; Kenyon et al. 1998; Ferreira et al. 2000; NagelkerkenI et al. 2000; Da Rocha et al. 2006). They provide oxygen and are involved in many mineralization and chemical cycling processes (Vidotti and Rollemberg 2004).

Seaweed beds in tropical areas are frequently associated with geological formations such as sandstone or biological reefs, which provide protection by dissipating the wave energy (Ferreira Júnior 2005). The local hydrodynamics can strongly affect the macrophytal and epiphytal biomass, abundance and density, which in turn affect the distribution and activity of organisms that are grazing on the seaweeds (Schanz et al. 2002). Seaweed beds provide protection from currents and desiccation and can influence the spatial distribution of the associated organisms (Muralikrishnamurty 1983). Moreover, seaweed beds also play a role in decreasing the current velocity and increasing the sedimentation rate of sediment and other particles present in the water column (Fonsêca and Calahan 1992). It has

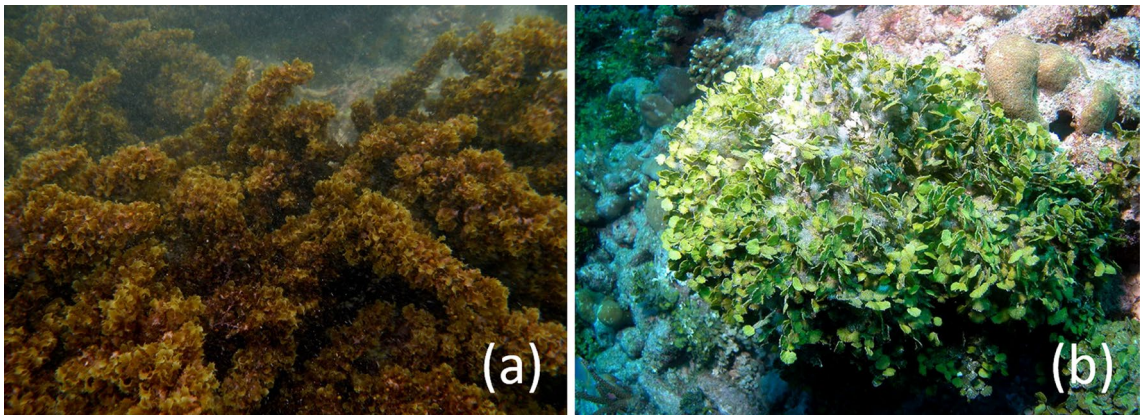

Fig. 1 **a** *Sargassum polyceratium* Montagne (1837) and **b** *Halimeda opuntia* (Linnaeus) Lamouroux (1816) (**a** modified after Olga Camacho and Jimena Samper Villareal, **b** courtesy Denis-Ader)

been suggested that the accumulation of detritus by the seaweed correlates with the ramification and structure of the macrophytes and increases microhabitat complexity, which would allow for a higher density of small-sized metazoans (Taylor 1967; Hicks 1980; Da Rocha et al. 2006). Seaweed beds are under the influence of tides and seasonality which also affect the associated organisms (Toyohara et al. 1999). However, for some small-sized organisms, examples are known where seasonality does not appear to be an important population driver, especially for those species which reproduce throughout the year (Coull and Vernberg 1975; Song et al. 2010).

Small-sized metazoans such as nematodes have a high capacity of colonizing seaweeds (Warwick 1977; Derycke et al. 2007) and play a fundamental role in the maintenance of the benthic ecosystem (Rieras and Hubas 2003). They are involved in processes such as biomineralization, bacterial population regulation, serve as food source for higher trophic levels and predate on the same and on lower trophic levels (Rysgaard et al. 2000; Schmid-Araya et al. 2002). With respect to seaweed, a very specific relationship with the associated fauna exists and can cause differentiation between communities from different seaweed species (Warwick 1977; Gibbons 1991; Gee and Warwick 1994a, b). Epistrate feeders are the most abundant nematode feeding type on seaweeds (Da Rocha et al. 2006) which may be related to the abundances of epiflora, and more specifically, of diatoms (Hagerman 1966; Tientjen and Lee 1973; Warwick 1977; Wetzel et al. 2002). Hence, nematodes may play an important role in controlling the densities of epiphytic organisms that compete for light and nutrients with the macroalgae (Van Donk 1998; Ghobrial et al. 2007). Information on temporal and spatial variation of nematode communities associated with seaweeds is extremely limited. Such a knowledge would provide insights on the dynamics of small-sized organisms associated with macrophytal ecosystems, allowing for a better understanding of physical factors that are important for structuring the communities.

In this study, the nematode communities associated with seaweed beds from the northeastern coast of Brazil were investigated. The seaweed species *Halimeda opuntia* (Linnaeus) Lamouroux (1816) and *Sargassum polyceratium* Montagne (1837) are abundantly present throughout the year. *H. opuntia* is a green calcareous seaweed that tends to make mats over hard substrate, while *S. polyceratium* is a brown seaweed which can stand up perpendicularly to the substrate (Fig. 1).

The specific goals of this study were fourfold. First, the diversity, community and feeding type structure of nematodes associated with *H. opuntia* and *S. polyceratium* were characterized and compared. Due to the different architectural structure of the two seaweed species, seaweed species-specific communities were expected. Moreover, a dominance of epistrate feeders was expected in the nematode communities of both seaweeds, because diatoms and cyanobacteria are abundant on the seaweed surface. Second, the temporal variability in nematode communities of *H. opuntia* and *S. polyceratium* was investigated by comparing the dry and rainy seasons and by comparing nematode communities over five months. Temporal fluctuations in abiotic parameters (e.g., the amount of rain, salinity) in Cupe beach may influence nematode abundances associated with *H. opuntia* and *S. polyceratium* and may cause shifts in the nematode community because of different tolerances of nematode species to abiotic changes. Third, spatial variation of nematode communities associated with *H. opuntia* in two transects parallel to the coast was investigated. These transects differed in their distance to the shore and in the degree of exposure to wave action. A

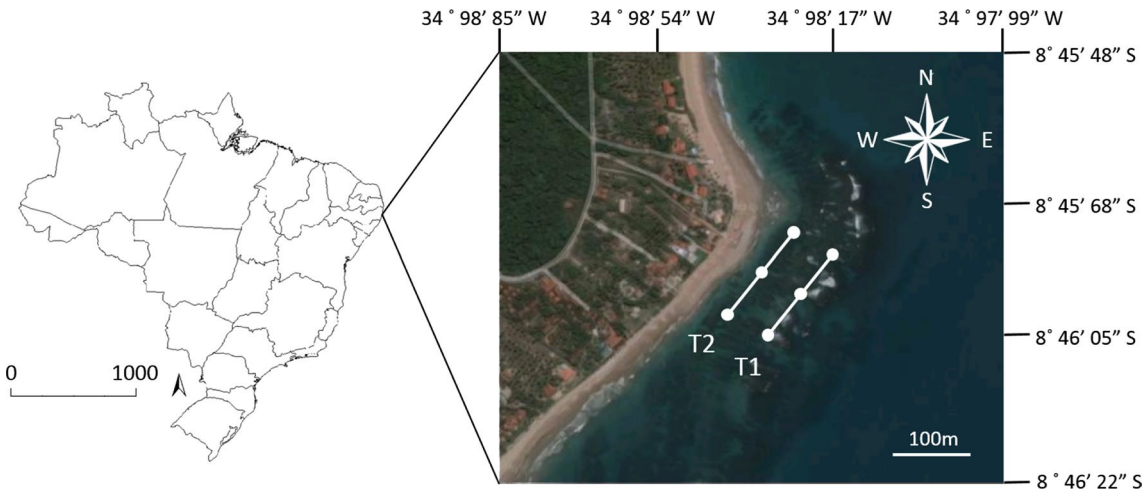

Fig. 2 Location of transects in Cupe beach—Ipojuca—Pernambuco at the northeast of the Brazilian coast. *T1* represents transect 1 which is more exposed to the waves, and *T2* represents transect 2 which is closer to the beach and thus less exposed to the waves (modified from Da Rocha et al. 2006)

higher variability in the nematode communities over time and lower nematode diversity and density were expected in the wave impacted zone because of the higher physical disturbance. Finally, the influence of sediment retention by the seaweeds *H. opuntia* and *S. polyceratium* on the nematode communities was assessed. The different architecture of *H. opuntia* and *S. polyceratium* may cause different sediment retention capacity, resulting in a higher density and richness of nematodes in the seaweed with the highest sediment retention capacity because of an increase in habitat complexity. Due to the tendency to form mats over hard substrate, it is expected that *H. opuntia* would accumulate more sediment.

Materials and methods

Study area

Cupe beach was chosen to test the impact of spatial and temporal variation and seaweed species on nematode communities. The beach is located in the northeast of the Brazilian coastline (coordinates 8°45′48″–8°46′22″S and 34°98′85″–34°97′99″W) and belongs to Ipojuca city, Pernambuco State. The beach is characterized by arenite and stone reefs with natural swimming pools separating the beach from the open sea. Various seaweed species occur on the sandstone and its surrounding areas in the subtidal and intertidal zone. The water temperature ranges from 27.0 to 28.7 °C and the salinity varies between 28.88 and 37.16 according to the season. The sediment is composed mainly of quartz sand and is very rich in bioclast, such as gastropod shells and pieces of calcareous algae (Dominguez et al. 1992).

Sample collection and processing

Based on their high abundance throughout the year, two species of seaweed were selected: *Sargassum polyceratium* and *Halimeda opuntia*. *S. polyceratium* and *H. opuntia* have architectural differences. The first one is a brown seaweed which can stand up perpendicularly to the substrate, whereas *H. opuntia* is a green calcareous seaweed that tends to make mats over hard substrate. The sampling occurred during the dry season (December 2005, January 2006) and the rainy season (May, June, July 2006) at low tide in the subtidal zone. Two transects of about 160 m length and parallel to the beach were demarcated with a distance between each other of about 80 m. Transect 1 (T1) was further from the shore compared to transect 2 (T2) (Fig. 2). For all five time points and for each transect, three equidistant sampling points were chosen, and from each point three samples from each seaweed species were collected (Fig. 2). The coordinates of each of the three sampling points are 8°45′78″S and 34°98′19″W, 8°45′86″S and 34°98′23″W, 8°45′94″S and 34°98′29″W for T1 and 8°45′73″S and 34°98′30″W, 8°45′81″S and 34°98′34″W, 8°45′87″ and 34°98′39″ for T2.

S. polyceratium only occurred in T2, while *H. opuntia* occurred in both transects. The seaweeds were collected by using a knife to detach the holdfast from the substrate, and the whole seaweed was put in a plastic bag and fixed with 4 % formalin. The seaweeds were washed under continuous water flow over a set of two sieves with mesh intervals for meiofauna of 500 and 44 micrometers and specimens retained on the latter were investigated. The volume of the seaweed was measured according to the methodology of Montouchet (1979) by measuring the difference

between the initial and final water volume after the inclusion of seaweed in a graduated cylinder. To test the sediment retention capacity of *S. polyceratium* and *H. opuntia,* the sediment that was retained by the sieves for each seaweed sample was put in Petri dishes, dried in an oven and weighted (g). The nematodes were counted under a dissection microscope Olympus SZ51. When present, at least 100 nematodes were randomly and manually picked out and mounted on slides for identification. In case less than 100 specimens were present in the sample, all were mounted on slides. Preparation and mounting of the nematode specimens occurred according to De Grisse (1969). The nematodes were identified under the light microscope Olympus CX31 to genus level by using the pictorial identification keys (Platt and Warwick 1983; Warwick et al. 1998) and dichotomous keys in Abebe et al. (2007). Additionally, the nematode community was classified according to the feeding types proposed by Wieser (1953) based on the buccal cavity morphology: 1A Selective deposit feeders, 1B non-selective deposit feeders, 2A epistrate feeders and 2B predators or omnivores.

Data analyses

The richness, densities and relative abundance of the nematode community per seaweed sample were calculated. To compare the temporal (dry and rainy period, both seaweeds) and spatial variation (*H. opuntia* only) of the nematode community associated with *S. polyceratium* and *H. opuntia*, the abundance of the nematode community was converted to density (individuals/ml), transformed to square roots and standardized by the total number of nematodes in the sample (relative abundance) before the similarity analysis. All multivariate analyses (nMDS, PERMANOVA and SIMPER) were performed based on Bray-Curtis similarity matrix using the software PRIMER v. 6.1.6 (Clarke and Gorley 2006). The fixed factors used in PERMANOVA were: seaweed species, season and transect (*H. opuntia* only). The factor month was treated as random variable and nested within the factor season. PERMANOVA was used to compare 1) the nematode community between *H. opuntia* and *S. polyceratium* occurring in the same transect over time (season [months]) and 2) compare the nematode community in both transects over time (season [months]) for *H. opuntia.* When significant differences were found, a SIMPER analysis was performed to determine the taxa that contributed to those differences. The amount of sediment retained by the seaweeds was standardized to g/ml. The standardized amount of sediment retained by the seaweed, nematode densities and nematode richness were fourth-root-transformed to fulfill the assumptions for a parametric test. Two-way ANOVAs were performed to test whether there were: 1) differences in nematode density and richness over time between the seaweeds in T2, 2) differences in nematode density and richness over time between transects for *H. opuntia*, 3) differences in sediment retention by *H. opuntia* over time between transect and 4) differences in sediment retention between the seaweeds over time in T2. To test whether the amount of retained sediment correlated with the nematode density on the seaweeds, a Spearman's correlation was done. The ANOVA and correlation analyses were performed using the statistical software STATISTICA v. 7 (StatSoft, Inc. 2004).

Results

Nematode communities and feeding type structure of *H. opuntia* and *S. polyceratium*

In total, 96 samples were analyzed: 35 for *S. polyceratium* (T2) and 61 for *H. opuntia* (T1 and T2). Identification of the nematode communities in these samples yielded 59 genera that were associated with both seaweeds (Table 1), 36 genera that were found only on *S. polyceratium* (T2: mean 6.74 ± 0.48) and 55 genera that were only associated with *H. opuntia* (T1: total = 49, mean 9.19 ± 0.61; T2: total = 41, mean 9.25 ± 0.75). The most abundant genera were *Euchromadora*, *Paracanthonchus* and *Halalaimus* for *H. opuntia* (35, 10 and 8 %, respectively), and *Euchromadora*, *Paracanthonchus* and *Hypodontolaimus* for *S. polyceratium* (34, 14 and 9 %, respectively). *Acanthonchus* and *Chromadora* reached two to threefold higher abundances in June compared to the other months, but only for *H. opuntia* (Fig. 3).

H. opuntia attained a significantly higher nematode richness (two-way, seaweed, ANOVA, $F = 13.04$, $P = 0.003$) compared to *S. polyceratium*. No significant compositional difference (PERMANOVA, seaweed, Pseudo-$F = 2.95$, $P = 0.057$) was observed between the nematode communities of both seaweeds (Table 2a).

The most frequent feeding type with more than 50 % of the relative abundance in both seaweeds were epistrate feeders (2A) (53 and 56 %), followed by predators (2B) (20 and 28 %), selective deposit feeders (1A) (20 and 14 %) and non-selective deposit feeders (1B) (7 and 3 %) in *H. opuntia* and *S. polyceratium,* respectively.

Temporal variation of nematode communities associated with *H. opuntia* and S. *polyceratium*

Comparing the nematode density pattern between *H. opuntia* and *S. polyceratium* over time in T2, no significant differences were observed within each season (two-way ANOVA, season × seaweed, $F = 0.25$, $P = 0.639$), but significant differences (Table 2a and Fig. 4a) were observed

Table 1 List of nematode genera relative abundance and feeding type associated with *H. opuntia* and *S. polyceratium* in Cupe Beach (Brazil) in 2005–2006

Genus	*H. opuntia* T1		*H. opuntia* T2		*S. polyceratium* T2		Feeding type
	Aver.	SE	Aver.	SE	Aver.	SE	
Acantholaimus	–	–	–	–	0.04	0.04	2A
Acanthonchus	12.50	±2.08	4.09	±1.33	8.85	±2.53	2A
Acanthopharyngoides	0.03	±0.03	–	–	–	–	2A
Adoncholaimus	1.27	±0.49	0.23	±0.17	1.05	±0.35	2B
Camacolaimus	–	–	0.32	±0.25	–	–	2A
Chromadora	16.52	±2.78	3.42	±0.95	5.51	±1.15	2A
Chromadorina	0.23	±0.17	0.26	±0.26	0.09	±0.09	2A
Chromadorita	0.31	±0.14	0.43	±0.24	0.07	±0.07	2A
Chromaspirina	0.12	±0.12	–	–	0.52	±0.52	2B
Crenopharynx	–	–	0.37	±0.37	0.59	±0.59	1A
Cyatholaimus	2.65	±1.13	1.51	±0.57	1.75	±0.79	2A
Demonema	–	–	0.17	±0.17	–	–	2B
Desmodora	0.88	±0.57	–	–	–	–	2A
Desmolaimus	0.15	±0.15	–	–	–	–	1B
Desmolorenzenia	0.41	±0.37	–	–	–	–	1A
Desmoscolex	0.35	±0.17	1.41	±0.96	–	–	1A
Draconema	16.23	±2.85	5.02	±1.21	0.17	±0.12	1A
Enoplus	0.23	±0.23	0.09	±0.09	–	–	2B
Epsilonema	0.61	±0.28	1.67	±0.97	–	–	1A
Euchromadora	16.35	±2.09	35.09	±3.13	34.33	±3.07	2A
Eurystomina	6.34	±1.27	2.08	±0.58	7.44	±1.70	2B
Gammanema	0.07	±0.07	0.16	±0.16	–	–	2B
Gammarinema	–	–	–	–	0.09	±0.09	2A
Graphonema	0.04	±0.04	–	–	0.33	±0.20	2A
Halalaimus	5.63	±1.26	7.64	±1.36	0.98	±0.40	1A
Halichoanolaimus	0.55	±0.20	0.97	±0.54	1.04	±0.64	2B
Hypodontolaimus	0.20	±0.16	0.28	±0.17	14.49	±3.76	2A
Marylynnia	–	–	1.65	±1.01	0.10	±0.10	2B
Metachromadora	0.12	±0.12	–	–	0.10	±0.10	2A
Metepsilonema	0.18	±0.13	0.25	±0.19	–	–	1A
Meyersia	0.05	±0.05	0.10	±0.10	0.35	±0.20	2B
Micoletzkyia	0.04	±0.04	–	–	–	–	1A
Oncholaimus	0.45	±0.33	–	–	0.29	±0.15	2B
Oxystomina	0.03	±0.03	–	–	–	–	1A
Paracanthonchus	5.56	±1.34	9.55	±2.39	9.19	±2.24	2A
Paracyatholaimoides	0.04	±0.04	–	–	–	–	2A
Paracyatholaimus	0.15	±0.11	0.44	±0.33	0.09	±0.09	2A
Pareurystomina	–	–	–	–	0.04	±0.04	2B
Phanoderma	0.26	±0.18	1.84	±1.19	0.06	±0.06	2A
Polygastrophora	1.02	±0.64	7.17	±3.70	2.75	±0.88	2A
Praeacanthonchus	0.11	±0.08	–	–	0.67	±0.53	2A
Prochromadorella	–	–	0.05	±0.05	–	–	2A
Prooncholaimus	1.13	±0.38	3.39	±1.13	1.55	±0.64	2B
Pseudochromadora	0.80	±0.43	1.44	±0.56	–	–	2A
Quadricoma	–	–	–	–	0.36	±0.36	1A
Sabatieria	1.68	±1.03	0.28	±0.15	0.03	±0.03	1B
Setoplectus	0.17	±0.17	–	–	–	–	1B
Sigmophoranema	0.17	±0.13	–	–	–	–	2A

Table 1 continued

Genus	*H. opuntia* T1		*H. opuntia* T2		*S. polyceratium* T2		Feeding type
	Aver.	SE	Aver.	SE	Aver.	SE	
Spiliphera	0.08	±0.08	0.18	±0.12	–	–	2A
Spilophorella	1.06	±0.36	1.21	±0.93	0.08	±0.08	2A
Spirinia	0.79	±0.48	0.46	±0.22	0.10	±0.10	2A
Symplocostoma	0.42	±0.18	2.94	±1.14	4.44	±1.02	2B
Synonchiella	0.12	±0.12	0.63	±0.45	–	–	2B
Synonema	0.95	±0.86	0.05	±0.05	0.06	±0.06	2A
Thalassomonhystera	0.38	±0.26	0.41	±0.26	–	–	1B
Thoracostoma	–	–	0.12	±0.12	0.10	±0.10	2A
Tricoma	0.27	±0.13	1.00	±0.51	–	–	1A
Viscosia	2.05	±0.61	1.48	±0.60	2.33	±1.69	2B
Wieseria	0.25	±0.25	–	–	–	–	1A

Feeding types: *1A* selective deposit feeders, *1B* non-selective deposit feeders, *2A* epistrate feeders, *2B* predators or omnivores (Wieser 1953)

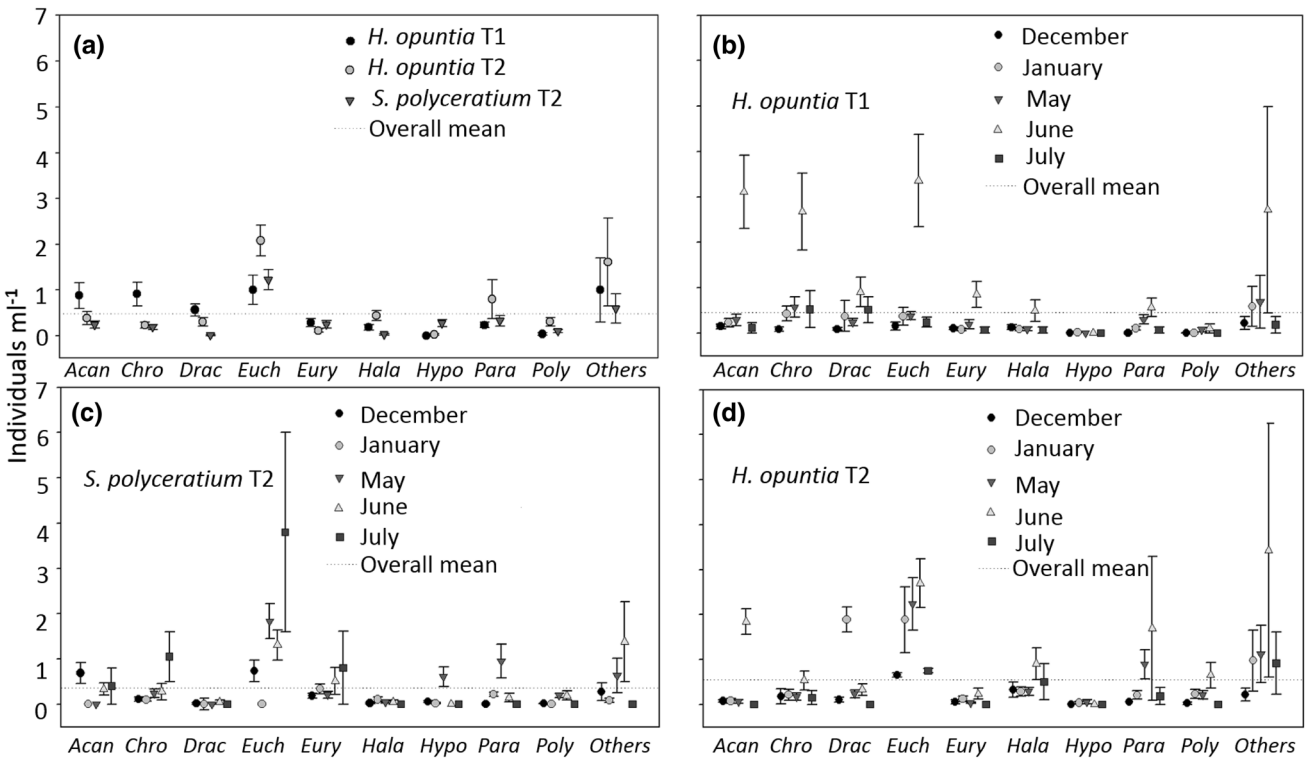

Fig. 3 Densities of the most abundant genera associated with *S. polyceratium* and *H. opuntia* in Cupe Beach (Brazil) in 2005–2006. **a** Overall average densities per seaweed and transect; **b–d** average densities of the most abundant genera per seaweed along the months of December, January, May, June and July. The corresponding abbreviations are: *Acan* (*Acanthonchus*), *Chro* (*Chromadora*), *Drac* (*Draconema*), *Euch* (*Euchromadora*), *Hala* (*Halalaimus*), *Hypo* (*Hypodontolaimus*), *Para* (*Paracanthonchus*) and *Poly* (*Polygastrophora*)

between the seaweeds within each of the five months (two-way ANOVA, month × seaweed, $F = 3.23$, $P = 0.029$). The pairwise comparison revealed that the nematode density in the month of June for *H. opuntia* (Table 4) was significantly higher compared with the months December, January and also higher than the data of June for *S. polyceratium* (Tukey HSD, *H. opuntia* January × *S. polyceratium* December; January; June = $P < 0.001$; $P < 0.001$; $P = 0.032$, respectively). No significant temporal variation in richness patterns (Fig. 4b) was observed (two-way ANOVA, season, $F = 2.58$, $P = 0.175$ – month,

Table 2 (a) ANOVA comparison of the nematode density, richness and seaweed retention capacity, and PERMANOVA comparison of the nematode community between *H. opuntia and S. polyceratium* in T2 over time; (b) ANOVA comparison of the nematode density, richness and seaweed retention capacity, and PERMANOVA comparison of the nematode community between the transects T1 and T2 for *H. opuntia* over time in Cupe Beach Brazil in 2005–2006

Dependent variable	Seaweed	Season	Month (nested in season)	Transect	Seaweed × season	Seaweed × month (nested in season)	Transect × season	Transect × month (nested in season)
Effect (F/R)	Fixed	Fixed	Random	Fixed	Fixed	Random	Fixed	Random
(a) *H. opuntia* and *S. polyceratium*								
Density	$F = 0.69$; $P = 0.452$	$F = 11.21$; $P = \mathbf{0.012}$	$F = 0.24$; $P = 0.861$	*	$F = 0.25$; $P = 0.639$	$F = 3.23$; $P = \mathbf{0.029}$	*	*
Richness	$F = 13.04$; $P = \mathbf{0.003}$	$F = 2.58$; $P = 0.175$	$F = 4.79$; $P = 0.115$	*	$F = 1.32$; $P = 0.272$	$F = 0.39$; $P = 0.754$	*	*
Sediment retention	$F = 10.53$; $P = \mathbf{0.010}$	$F = 0.05$; $P = 0.828$	$F = 1.41$; $P = 0.391$	*	$F = 0.09$; $P = 0.761$	$F = 0.67$; $P = 0.572$	*	*
Community structure	$F = 2.954$; $P = 0.057$	$F = 3.45$; $P = \mathbf{0.002}$	$F = 2.62$; $P = \mathbf{0.001}$	*	$F = 1.60$; $P = 0.133$	$F = 1.54$; $P = 0.066$	*	*
(b) *H. opuntia*								
Density	*	$P.F = 0.88$; $P = 0.413$	$P.F = 13.81$; $P = \mathbf{0.029}$	$P.F = 1.72$; $P = 0.248$	*	*	$P.F = 0.37$; $P = 0.571$	$P.F = 1.21$; $P = 0.314$
Richness	*	$P.F = 3.56$; $P = 0.114$	$P.F = 1.33$; $P = 0.408$	$P.F = 0.09$; $P = 0.769$	*	*	$P.F = 1.36$; $P = 0.285$	$P.F = 0.65$; $P = 0.584$
Sediment retention	*	$P.F < 0.001$; $P = 0.987$	$P.F = 2.35$; $P = 0.250$	$P.F = 0.40$; $P = 0.539$	*	*	$P.F = 0.73$; $P = 0.416$	$P.F = 0.46$; $P = 0.707$
Community structure	*	$P.F = 1.10$; $P = 0.391$	$P.F = 1.97$; $P = \mathbf{0.004}$	$P.F = 5.57$; $P = \mathbf{0.045}$	*	*	$P.F = 1.56$; $P = 0.263$	$P.F = 0.75$; $P = 0.82$

The significant differences are marked in bold

* Variable not tested because *S. polyceratium* only occured in T2

Table 3 (a) PERMANOVA pairwise comparison of the *H. opuntia* and *S. polyceratium* nematode community between the studied months; (b) ANOVA pairwise comparison of the nematode densities between the months of T1 and T2 for *H. opuntia* in Cupe Beach, Brazil, in 2005–2006

	December	January	May	June	July
(a)					
December					
January	**0.004**				
May	**0.001**	**0.032**			
June	**0.012**	**0.001**	**0.001**		
July	0.055	0.115	**0.006**	0.438	
(b)					
December					
January	**0.005**				
May	**0.036**	1.000			
June	**<0.001**	**<0.001**	**<0.001**		
July	0.700	0.805	0.800	**<0.001**	

The significant differences are marked in bold

$F = 4.79$, $P = 0.115$ – season × seaweed, $F = 1.32$, $P = 0.27$ – month × seaweed, $F = 0.39$, $P = 0.754$).

In terms of community structure, no clear distinction was observed in the nMDS plot (Fig. 5). No significant interaction between seaweed and seasons (PERMANOVA, seaweed × season, Pseudo-$F = 1.60$, $P = 0.133$) or seaweed and months (PERMANOVA, seaweed × months Pseudo-$F = 1.54$, $P = 0.066$) was observed, indicating that community structure between seaweed species over time was similar. However, nematode community structure was significantly different between the dry and rainy seasons (PERMANOVA, season, Pseudo-$F = 3.45$, $P = 0.002$). The genera that contributed the most for the differences between seasons were *Euchromadora*, *Chromadora* and *Acanthonchus* (SIMPER, 12.78, 7.75, and 7.69 %). Moreover, nematode communities were also significantly different between the months (PERMANOVA, month, Pseudo-$F = 2.62$, $P = 0.001$). Pairwise comparisons revealed that the nematode community significantly fluctuated over the months (Table 3a).

Spatial variation of the nematode community of *H. opuntia*

A total of 49 and 41 genera were found associated with *H. opuntia* in T1 and T2, respectively. The genera that presented the highest densities were *Euchromadora, Chromadora* and *Acanthonchus* in T1 (1.01; 0.91; 0.88 individuals/ml, respectively) and *Euchromadora*, *Paracanthonchus*

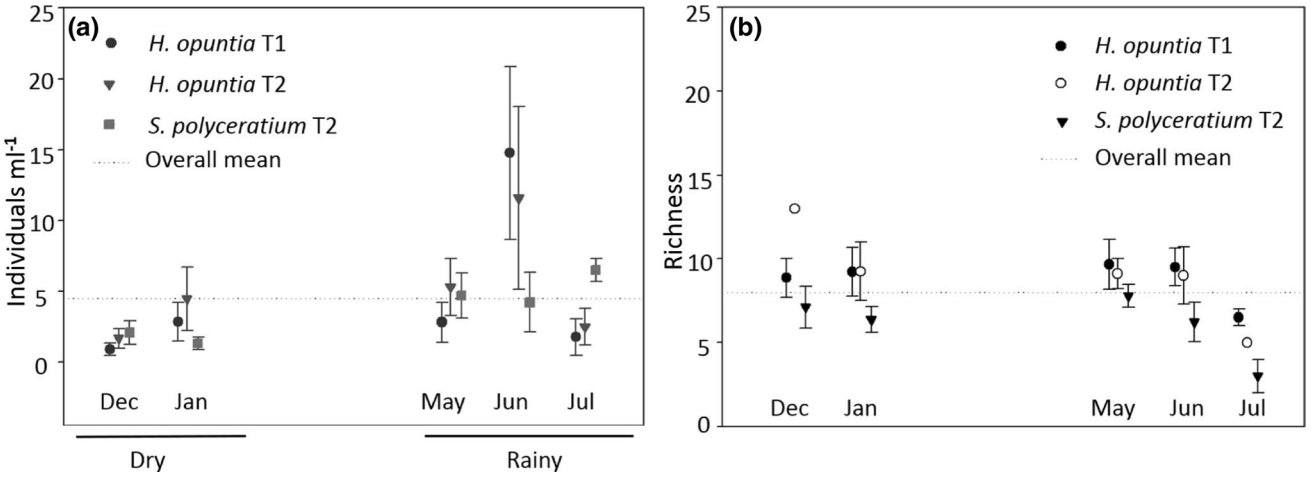

Fig. 4 Temporal and spatial average **a** densities and **b** richness of the nematode community associated with *H. opuntia* (*T1* and *T2*) and *S. polyceratium* (*T2*) in Cupe Beach (Brazil) in 2005–2006

and *Halalaimus* in T2 (2.07; 0.80; 0.44 individuals/ml, respectively). The genera that reached the highest relative abundance in each transect (Fig. 6) were *Chromadora, Euchromadora* and *Draconema* in T1 (17, 16, and 16 %, respectively), and *Euchromadora*, *Paracanthonchus* and *Halalaimus* in T2 (35, 10, and 8 %, respectively).

No significant differences in nematode density (two-way ANOVA, season × transect, $F = 0.37$, $P = 0.571$ − month × transect, $F = 1.21$, $P = 0.314$) or richness (season × transect, $F = 1.36$, $P = 0.285$ − month × transect, $F = 0.65$, $P = 0.584$) between both transects over time were observed, indicating that the observed pattern in density and richness was very similar over time in both transects (Table 2b). No significant difference in nematode density (two-way ANOVA, transect, $F = 1.72$, $P = 0.248$) or richness (two-way ANOVA, transect, $F = 0.09$, $P = 0.769$) between the T1 and T2 was found. For the factor time, only a significant difference in nematode density between the months was observed (two-way ANOVA, month, $F = 13.81$, $P = 0.029$, Table 3b). The nMDS plot did not show a clear separation between transects (Fig. 7), and the interaction between the transects and season or transects and months did not show a significant difference over time (PERMANOVA, transect × season, Pseudo-$F = 1.56$, $P = 0.263$; transect × month, Pseudo-$F = 0.75$, $P = 0.820$). However, the main effects were significantly different (Table 2b), revealing a difference in community structure between the two transects. (PERMANOVA, transect, Pseudo-$F = 5.57$, $P = 0.045$) and months (PERMANOVA, month, Pseudo-$F = 1.97$, $P = 0.004$). The taxa that contributed the most for the differences between transects were *Euchromadora*, *Chromadora* and *Draconema* (SIMPER: 8.13, 8.06, and 7.57 %, respectively), with the last two being more abundant in T1, while *Euchromadora* was more abundant in T2. The pairwise analysis revealed that the differences in months for both transects were between May and June (PERMANOVA, pairwise, $P = 0.001$). The genera that contributed the most for the differences were *Paracanthonchus*, *Euchromadora* and *Acanthonchus* (SIMPER: 9.03 %; 8.09 %; 8.01 %, respectively), with the two first more abundant on May.

Comparison on sediment retention between seaweeds and for *H. opuntia between* transects

In total, 90 samples for *H. opuntia* (9 replicates per transect over 5 months) and 35 samples for *S. polyceratium* were analyzed. There were no differences in sediment retention over time between *H. opuntia* and *S. polyceratium* in T2 (two-way ANOVA, seaweed × season, $F = 0.09$, $P = 0.761$ − seaweed × month, $F = 0.67$, $P = 0.572$). Yet, the difference in architecture of the two seaweeds yielded differences in overall sediment retention capacities in T2 (Table 2a) where *H. opuntia* retained significantly more sediment than *S. polyceratium* (two-way ANOVA, seaweed, $F = 10.53$, $P = 0.010$). No significant differences between season (two-way ANOVA, season, $F = 0.05$, $P = 0.828$) or between months (two-way ANOVA, month, $F = 0.41$, $P = 0.391$) were observed. For *H. opuntia,* no spatial pattern (Table 2b) was observed in sediment retention between transects over time (two-way ANOVA, transect × season, $F = 0.73$, $P = 0.416$ – transect × month, $F = 0.46$, $P = 0.707$) or between the transects (two-way ANOVA, $F = 0.40$, $P = 0.539$). Performing the Spearman's correlation, no correlation was found between the

Table 4 ANOVA pairwise comparison of the nematode densities between seaweeds, season and months in Cupe Beach, Brazil, in 2005–2006

Seaweed	Season	Month	*H. opuntia*	*H. opuntia*	*H. opuntia*	*H. opuntia*	*H. opuntia*	*S. Polyceratium*	*S. Polyceratium*	*S. Polyceratium*	*S. Polyceratium*	*S. Polyceratium*	*S. Polyceratium*
			Dry	Dry	Rainy	Rainy	Rainy	Dry	Dry	Rainy	Rainy	Rainy	Rainy
			December	January	May	June	July	December	January	May	June	July	
H. opuntia	Dry	December											
H. opuntia	Dry	January	0.952										
H. opuntia	Rainy	May	0.909	1									
H. opuntia	Rainy	June	0.110	0.270	0.285								
H. opuntia	Rainy	July	0.999	0.999	0.999	0.721							
S. Polyceratium	Dry	December	1	0.411	0.229	**<0.001**	0.999						
S. Polyceratium	Dry	January	0.999	0.207	0.094	**<0.001**	0.998	0.999					
S. Polyceratium	Rainy	May	0.933	1	1	0.230	0.999	0.286	0.123				
S. Polyceratium	Rainy	June	0.997	0.998	0.989	**0.032**	1	0.820	0.562	0.995			
S. Polyceratium	Rainy	July	0.935	0.999	0.999	0.999	0.997	0.784	0.668	0.999	0.993		

The significant differences are marked in bold

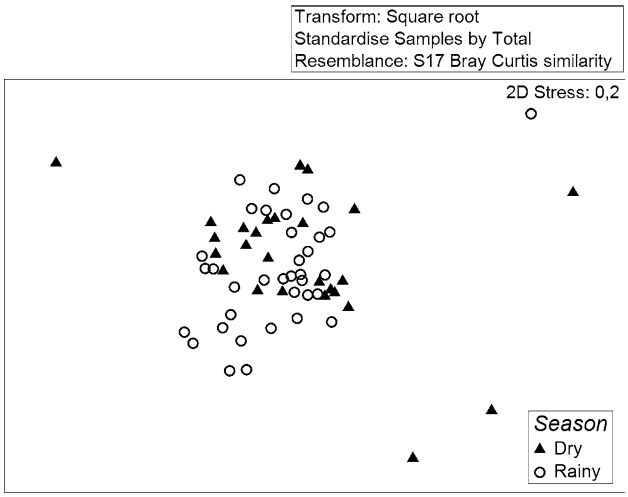

Fig. 5 Non-metric MDS comparing the nematode communities between the dry and rainy season for both seaweeds *H. opuntia* and *S. polyceratium* in Cupe Beach (Brazil) in 2005–2006

nematode density and the amount of sediment retained for *H. opuntia* or *S. polyceratium*. However, a positive correlation was observed between the amount of retained sediment and nematode richness for both seaweeds (*H. opuntia*: $R = 0.32$, $P = 0.011$—*S. polyceratium*: $R = 0.40$, $P = 0.014$). Three of the most abundant genera showed a positive correlation between the amount of retained sediment and genus density in both seaweeds: *Draconema* (*H. opuntia*, $R = 0.26$, $P = 0.03$—*S. polyceratium*, $R = 0.34$, $P = 0.04$), *Euchromadora* (*H. opuntia*, $R = 0.41$, $P < 0.001$—*S. polyceratium*, $R = 0.37$, $P = 0.02$) and *Paracanthonchus* only in *H. opuntia* ($R = 0.28$, $P = 0.026$). No correlation was found for *Acanthonchus*, *Chromadora*, *Eurystomina* or *Hypodontolaimus*.

Discussion and conclusions

Co-occurring seaweed species harbor similar nematode communities and similar trophic composition

Overall nematode densities, community structures and community compositions were similar on both seaweeds, which is in agreement with the observations described in a study involving four different macrophyte species (Da Rocha et al. 2006). Despite the similarity in density and community structure (P value = 0.057 fairly in the limit), the genera richness was significantly different between *H. opuntia* and *S. polyceratium*. In terms of average relative abundance, some nematodes appeared to prefer one seaweed species over the other as illustrated by *Hypodontolaimus* for *S. polyceratium*. In contrast, on *H. opuntia* a higher average relative abundance of the

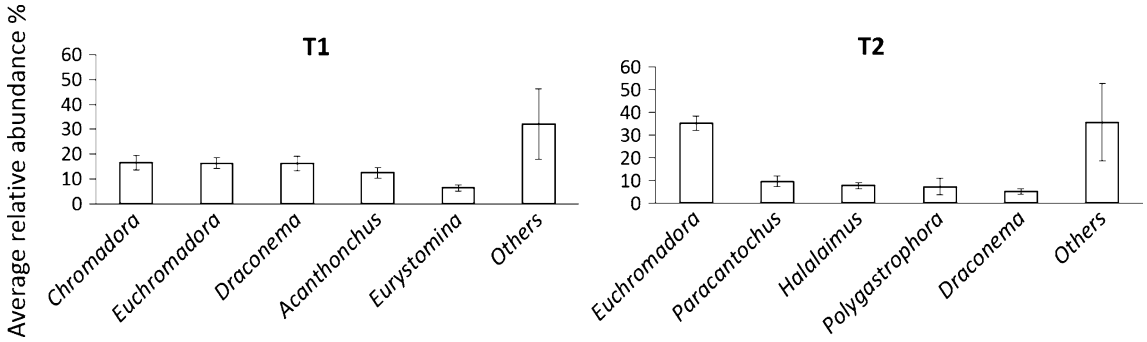

Fig. 6 Average relative abundance of the five most abundant genera associated with *H. opuntia* in both transects in Cupe Beach (Brazil) in 2005–2006

family Draconematidae was observed, also the occurrence of Epsilonematidae, which were not associated with *S. polyceratium*. Both families are typically found associated with corals and other hard substrate (Raes and Vanreusel 2006; Raes et al. 2008; Armenteros et al. 2012); their occurrence on *H. opuntia* is most likely related to the calcareous nature of *H. opuntia*. This kind of preference was already mentioned by other authors (Hopper and Meyers 1967a, b; Warwick 1977). In epiphytic amphipods, no correlation has been found between seaweed morphology or complexity (ratio between surface area and biomass) and their abundance or species richness (Russo 1990). In contrast, ostracod species from California did show a strong correlation with complexity levels of the seaweed they were associated with (Frame et al. 2007). Therefore, it seems that different organisms have a different relationship with the macroalgal substrate. Regarding the feeding types, in this study, the epistrate feeders (2A) were the most dominant in both seaweeds, as has been previously observed for seaweeds (Ólafsson et al. 1995; Da Rocha et al. 2006; Jaya et al. 2012). However, this is in contrast with the nematode community associated with the seagrass *Zostera* in which 1B was the most dominant feeding type (Alves et al. 2015) and with *Caulerpa taxifolia* which was dominated by the genus *Halichoanolaimus,* a predator/omnivore or 2B (Soetaert and Heip 1995; Pape et al. 2013).

Seasonal variation reveals higher nematode abundances during the rainy season, but the community composition was very similar

Overall nematode density was significantly higher during the rainy season and varied differently among months on both seaweeds. In June, *H. opuntia* presented a significantly higher nematode density compared with *S. polyceratium* in the same month. Although the same general trend was observed for both seaweeds (increase of nematode density toward June), the magnitude of this increase appeared to be seaweed species specific. Temporal variation in density of nematodes associated with seaweeds peaking in certain periods of the year has already been observed (Kito 1982). However, comparisons between nematode communities from different seaweeds species over time are extremely rare. In the current work, no variation in richness was observed between seasons and months for both seaweeds and for *H. opuntia* in both transects, showing a fairly stable composition throughout the year. In contrast, a significant difference in nematode community structure has been found between the rainy and the dry seasons. Although the composition was very similar between the dry and rainy seasons, some abundant genera reached significantly higher relative abundances during the rainy season (e.g., *Euchromadora*). Temporal variation of the epifauna living on macrophytes can be related to seasonal change of the thallus (Travizi et al. 2004) or

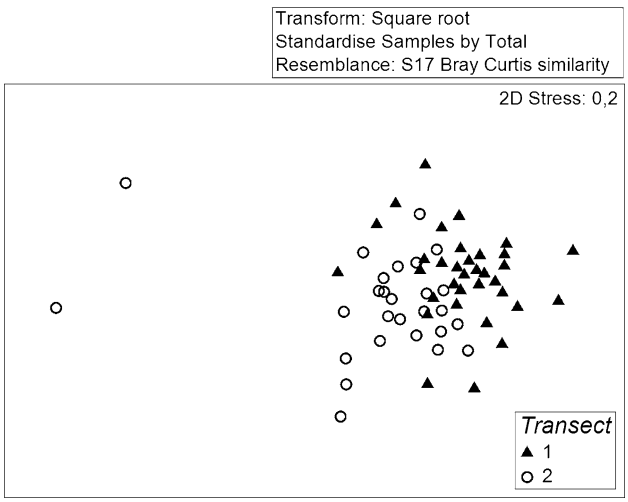

Fig. 7 Non-metric MDS comparing the nematode communities between the two transects for *H. opuntia* in Cupe Beach (Brazil) in 2005–2006

to preferences for different structures of the seaweed (Venekey et al. 2008). Microarthropod species associated with the macrophyte *Ascophyllum nodosum* have also shown temporal variation (Jarvis and Seed 1996), with some species showing an increased density at a particular time point while the density decreased for other species. Meiofauna associated with the seagrass *Posidonia oceanica* showed higher temporal variability in density present on the leaf region than on the stem region, where the densities were higher with little variation throughout the year (Novak 1982). These differences were correlated with the seasonal development of the seagrass. Seaweeds, as *Sargassum muticum*, also show seasonal developmental variation which in turn may affect the associated fauna (Taylor 1997; Baer and Stengel 2010). However, it is important to emphasize that the mentioned studies were performed in temperate higher latitudes (>42°N or >35°S) where there is a marked seasonal variation affecting the organism's life cycle. In contrast, the current work was performed in a tropical low latitude (8°S) region with fairly stable temperatures averaging at 26.5 °C during the rainy season and at 27.9 °C during the dry season (Machado 2015).

The nematode community structure differed between transects, but no differences in the density or richness were observed

Although there were no significant differences in nematode density or richness, for *H. opuntia* between transects, there was a significant difference in nematode community structure. Spatial variation on epiphytic meiobenthic communities has been attributed to food source availability and environmental complexity (Novak 1982; Bell et al. 1984). The level of shelter from wave action appears to be a factor influencing nematode communities associated with the seaweed *Sargassum* in Brazil (Venekey et al. 2008) and with *Gelidium pristoides* in South Africa (Gibbons 1988). However, such effect of wave exposure was not observed by Arroyo et al. (2004) studying the meiofauna and nematode community associated with the seaweed genus *Laminaria* in Spain. In the present investigation, *Euchromadora* was the genus that contributed most to spatial differences; it preferred areas closer to the beach and thus more sheltered (T2), where it could reach twice the density of the area further away from the beach line (T1). This may indicate that the changes in community structure were mostly resulting from a higher degree of exposure rather than from temporal fluctuation. The community associated with macrophytes reached a higher average density in more sheltered areas, although the data were not always statistically significant.

Sediment retention capacity differed between seaweeds, affecting the density of some specific genera but not the density of the whole community

There was no significant difference in sediment accumulation between the two transects over time. The sediment retention capacity related more to the seaweed species rather than to degree of exposure and appears to be also related to the level of architectural complexity of the seaweed. Despite a significant difference in sediment retention capacity of the two seaweeds studied, the overall nematode density on the seaweeds was not affected. However, the retained sediment showed a positive correlation with the nematode richness for both seaweeds (*H. opuntia*: $R = 0.32$; $P = 0.011$—*S. polyceratium*: $R = 0.40$; $P = 0.014$). For some genera, a positive correlation was observed between nematode density and seaweed species, for example in *Draconema* and *Euchromadora*. This may suggest that the effect of the amount of retained sediment is species specific, affecting the community structure and richness, but not the overall nematode density. Interestingly, *Draconema* and *Euchromadora* did not occur in the bottom sediment (de Oliveira et al. 2014), maybe due to morphological and locomotion adaptations of the former (Raes et al., 2008), while *Hypodontolaimus* occurred in the bottom sediment and on the seaweed but did not show any correlation with the retained sediment. This suggests that the retained sediment by the seaweed was a more important factor affecting the nematode genera that were restricted to seaweeds rather than the genera occurring in seaweed and sediment. This result contrasts with two general paradigms described in a number of articles (Wieser 1951, 1952; Ott 1967; Hopper and Meyers 1967a, b; Moore 1971; Warwick 1977; Da Rocha et al. 2006): (1) the more sediment on the seaweed, the higher the density of nematodes and (2) the more sediment, the more nematodes originating from the sediment are also found on the seaweed. However, none of the above mentioned studies quantified the amount of retained sediment and tested its correlation with the nematode community density or structure on seaweeds. Nematodes choose actively the substrate on which they settle (Ullberg and Ólafsson 2003; Arroyo et al. 2006) and are rather not just passively transported along with the sediment through currents and retained by the seaweed. Experiments on colonization of macrophytes by nematodes have demonstrated that through time, the community is dominated by species that are typically found associated with macrophytes (Arroyo et al. 2006; Derycke et al. 2007). This result opposes the idea that the more sediment retained by the seaweed, the higher the nematode overall density and the higher the number of nematodes originally coming from the sediment.

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